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Biology and outbreaks of *Microdiprion pallipes* (Hymenoptera; Diprionidae) in Sweden

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Abstract

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During outbreaks, *Microdiprion pallipes* (Fall.) is the most destructive of the pine sawflies in Sweden. Its distribution includes most provinces, but damaging outbreaks have until recently occurred only in two inland areas in northern Sweden. These areas are characterised by high elevation, a harsh climate, and slow tree growth. The four recorded outbreak periods showed a 10 year periodicity. Outside these areas, a lesser outbreak occurred in 1988 to 1990, on the east coast (province of Uppland).

Outbreak patterns, life history variation, and mortality factors were studied. Factors that may explain the distribution of outbreaks and the population patterns were identified. Experimental and observational evidence on the potential of various factors to influence fecundity, dispersal, and survival was evaluated.

In the outbreak areas, there were few major population factors. Parasitism by *Rhorus substitutor* (Thunb.) was the largest cause of larval mortality and the only important density-dependent mortality factor.

The different diapause strategies of *M. pallipes* and *R. substitutor* may contribute to stabilise this system. Different flight periods of the host and the parasitoid may explain a possible correlation between weather and outbreaks.

Elsewhere in Sweden, where low population densities prevail, there may be similarities in population processes between *M. pallipes* and the other widely distributed diprionids with solitary larvae, which never have attained outbreak densities in Sweden. Interactions with other diprionids through shared natural enemies may be an important population process and may influence the distribution of outbreaks.

Keywords: Distribution, life history, fecundity, mortality, damage, *Pinus sylvestris*, *Pinus contorta.*

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Introduction

Microdiprion pallipes (Fall.) (Hymenoptera; Symphyta; Diprionidae) is the only pine sawfly that, in recent years, has caused significant tree mortality on reforestation areas in Sweden. It is the least studied of the pine-defoliating sawflies that are important to forest management (Olofsson, 1985).

M. pallipes consists of two allopatric subspecies (Forsslund, 1960). The southern, *M. pallipes polita* (Klug), subsequently referred to as *M. polita*, occurs in alpine regions of Germany, Switzerland, and Austria. The larvae feed mainly on *Pinus montana* Mill. but also on *Pinus cembra* L. and *Pinus sylvestris* L. The few reported outbreaks have occurred in *P. sylvestris* stands. *M. polita* has been studied by Scheidter (1923), Mallach (1973; 1974*a*; 1974*b*), and Pschorn-Walcher (1962; 1987). The northern, *M. pallipes pallipes*, subsequently referred to as *M. pallipes*, has been recorded from Poland, northern Germany, Scotland, Denmark, Norway, Sweden, Finland, through Sibiria to Sakhalin (Viitasaari & Varama, 1987), and from England (Wright, 1987). Damaging outbreaks have been reported mainly from Sweden, Finland, and Norway. *P. sylvestris* is the native host but it has also been found on the introduced *Pinus contorta* Dougl. (Annila, Heliövaara, Puukko & Rousi, 1983). The biology of *M. pallipes* has been studied by Forsslund (1960).

The earliest described outbreak of *M. pallipes*, which is the only known outbreak in Denmark, occurred in 1872–1873 (Borries, 1886). In Finland outbreaks were observed in 1902–1903 (Elfving, 1904) and have since been few and localised (Viitasaari & Varama, 1987). Outbreaks have also been reported from Norway (Ehnström, Bejer-Petersen, Löyttyniemi & Tvermyr, 1974; Austarå, Annila, Bejer & Ehnström, 1983).

In Sweden, *M. pallipes* has been recorded from Skåne in the south to Lapland in the north, but it is rare in the southern provinces. Outbreaks have occurred in northwest Dalarna and in highland areas of Lapland between the mountains and the coastal region, at altitudes of 300 to 800 m (Fig. 1). The first known outbreak was observed in Dalarna in 1952. It was described as a 'permanent outbreak' (Forsslund, 1960). In Lapland, three outbreak periods have been reported: 1956–58 (Forsslund, 1960), 1966–67 (Christiansen, 1969), and 1975–76 (Löyttyniemi, Austarå, Bejer & Ehnström, 1979). The areas in Dalarna and Lapland with frequent high populations will collectively be referred to as the outbreak areas. The only known outbreak in other regions occurred in the province of Uppland from 1988 to 1990.

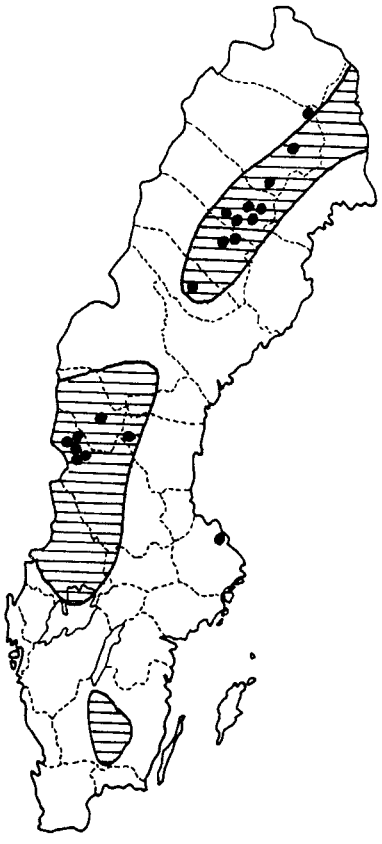

Fig. 1. Distribution of *M. pallipes* outbreaks in Sweden 1952–1992. Areas larger than 1 hectare with at least some tree mortality are included. The zones with a continental-type climate are hatched (from Ångström, 1958).

Little is known about the causes of the population fluctuations of *M. pallipes*. Forsslund (1960) associated a large increase in parasitism with the decline of the outbreaks. In the present paper, covering the period from 1974 to 1993, a large number of observational and experimental results are reported as a first step toward understanding the population dynamics of *M. pallipes*.

The aim of the study was to identify factors with a potential to cause major population change and factors that may explain the differences in population dynamics between outbreak and non-outbreak areas. In particular, outbreak patterns, life history variation, and mortality factors were investigated. Based on the results, hypotheses on the population processes were developed as a basis for further studies and for evaluating population management options.

Methods

In the outbreak areas in the province of Dalarna, northwest of Särna (61°40′N, 13°05′E), larvae were sampled in 1974–1978, 1984, and 1990. In Lapland, near Arvidsjaur (65°35′N, 19°15′E), larvae were sampled in 1975, 1976, 1985, and 1987. Four areas in the province of Uppland were sampled: outbreak populations at Stångskäret and Hällberget at the east coast near Forsmark (60°23′N, 18°10′E) in 1989–1991, and low-density populations at Vattholma, northeast of Uppsala (60°2′N, 17°45′E), in 1989–1991 and at Västland (60°25′N, 17°37′E) in 1989. Rearings before 1980 were kept in a greenhouse at natural light (59°35′N), and cocoons were overwintered in an outdoor cage. From 1980, they were kept at 23°C and a 22 h light period (350 lux), and cocoons were overwintered at 4°C, 10 h. Emergence from cocoons was recorded daily. Remaining intact cocoons were opened and their contents analyzed. Groups of 100 cocoons were used unless specified. Data and observations concern the Uppland population at Stångskäret when no site is mentioned. The methods are arranged according to the developmental stage of the insect. In studies requiring few details on methods, these are included in the results. Data in the text are mean ± SD and range.

Eggs

An egg sample consisted of the previous year's growth at a branch-tip. The egg position was measured from the tip of the needle to the leading edge of the egg pocket, and from the needle sheath to the base of the shoot. Eggs per centimetre of shoot length was determined for the egg-bearing section of the shoot.

Host suitability for oviposition and egg development was studied by enclosing a male and a female in a plastic bag on cut foliage. Four types of Scots pine foliage were tested: 0.5 m tall trees on a sun-exposed site, mature trees with small, sun-exposed needles, mature trees with large, coarse, sun-exposed needles, and 5 m tall trees with soft, shaded needles. One sample from each of ten trees of similar phenotypes were tested in each group.

Larvae

Larvae were collected by beating branches or small trees over a piece of cloth. One sample was taken for each date and site. To study the timing of parasitoid attack with larval development, four samples were taken during the larval period in 1989 and three in 1990. Samples to compare parasitism and diapause levels were taken when most larvae were in their third to fifth stages. They were reared to cocoons in the laboratory. After 1 month, they were overwintered during 6 months and then reared to emergence.

A survey was made to find pathogens of potential use in biological control. Larvae sampled during 1974–1992 from Lapland ($n=2\,730$), Dalarna ($n=3\,960$), Uppland ($n=10\,620$), and other sites ($n=240$), which were reared to cocoon spinning in the laboratory, were included. Larvae in the field samples and in the rearings, that showed signs of disease, were examined for the presence of pathogens in various tissues.

Infectivity of nuclear polyhedrosis viruses (NPV) from *Neodiprion sertifer* (Geoffr.), *Neodiprion lecontei* (Fitch), and *Gilpinia hercyniae* (Htg.) and the insect pathogenic fungus *Beauveria bassiana* Vuill were tested. Pieces of foliage were immersed in NPV suspensions containing 106 polyhedral bodies per millilitre. Each virus was tested on four groups of 15 third instar larvae. A strain of *B. bassiana*, isolated from *N. sertifer* larvae, was grown on Saboraud agar plates. Pieces of foliage were contaminated with high, unspecified amounts of spores harvested from these plates. Third instars, in 14 groups of 11 larvae, were tested.

Cocoons

Searches of litter and vegetation yielded too few cocoons, in relation to the calculated density, to

develop a sampling procedure. Therefore, laboratory-reared cocoons were used to estimate field mortality both in 1989 and 1990. When most larvae had left the trees, large cocoons (mainly females, $n = 135$) were placed in the litter. Three cocoons, individually attached by wire loops, were put in various positions within the crown projection of a tree. They were checked in late autumn and repositioned (in 1989) or replaced (in 1990). Cocoons removed during autumn were overwintered at 4°C. In spring, before emergence began, all cocoons were removed and checked for signs of predation or exit holes. Autumn and spring samples were then reared to emergence.

The diapause in the cocoon was studied by varying the length of the cold period. Cocoons were obtained from field-collected larvae. One month after spinning, they were transferred to overwintering conditions. At intervals, 100 or 200 cocoons were removed and reared to emergence. For comparison with field conditions, a wire cage with cocoons was put in litter on 22 July 1989. Samples were removed at intervals during the following spring and reared to emergence.

The effect of the photoperiod on diapause was studied by rearing larvae from their third stage onwards at daily light periods of 22, 18, 14, and 10 hours. About a month after spinning, the cocoons were overwintered during 9 months and then reared to emergence. Additional diapause data were obtained from the field samples in 1989 and 1990.

Adults

In feeding tests, adults had access to a water solution of 2.5 per cent glucose and 2.5 per cent fructose. This method was previously used successfully with *N. sertifer* (unpublished). In a 9 cm petri dish, an adult was provided with a dispenser. It consisted of a glass tube sealed with cotton that became moistened by the liquid. To study the behaviour of the adults, the liquid was also given as drops in the dish both to freshly emerged sawflies ($n = 10$) and to sawflies kept dry during 3 days ($n = 10$).

Fecundity was determined by counting the eggs in the ovaries of newly emerged females. In females that were allowed to oviposit, both the deposited eggs and those remaining in the ovaries were counted.

Results

Distribution and outbreaks

The distribution records of diprionids are largely based on field observations of larvae. As museum specimens are rarely available to substantiate such records, observations of *M. pallipes* larvae in Sweden made since 1952 were listed (Table 1). The records in Forsslund (1960) and observations made or verified by the author were included.

High population densities have occurred periodically in the outbreak areas in Lapland and northwestern Dalarna (Fig. 1). At Arvidsjaur, where there have been four outbreaks since 1952, the results indicate a 10-year outbreak cycle. The outbreaks have tended to occur during periods with below average summer temperatures (Fig. 2). The most recent outbreak occurred in 1985–1987 around Arvidsjaur and Malå, damaging about 500 ha of young pine stands. Young trees up to about 1.5 m in height, on sites characterised by high elevation, adverse climate, and slow tree growth, suffered the most severe damage.

In the vicinity of the outbreak areas there have been a few, localised outbreaks (Table 1). The only outbreak in other regions began in Uppland in 1988. The site contrasted with the outbreak areas in being near the coast at elevations below 25 m and having a local climate of a maritime type. The outbreak persisted through 1990. Damage was not severe in 1991 and 1992, but the populations remained at levels higher than those observed outside the outbreak areas. In 1993, all populations in Uppland had subsided to very low levels. The highest larval densities occurred in 1–3 m tall stands, while there were no attacks in lower stands. Many of the attacked trees were of a vigorous growth type, quite different from the slow-growing trees in the outbreak areas. Some larvae were found on sun-exposed low branches of mature trees.

Other observations of larvae were made at variously disturbed sites, e.g. along forest roads and in abandoned gravel pits (Table 1). Scattered trees often were severely damaged but

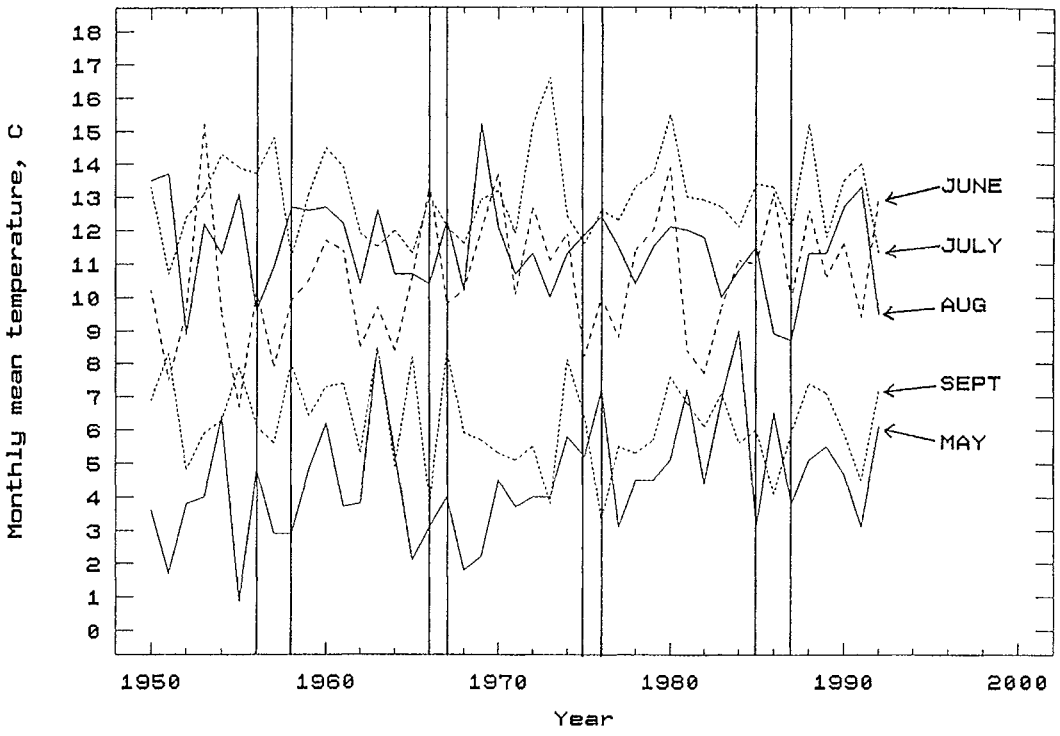

Fig. 2. Monthly mean temperatures near the Arvidsjaur area (at Arjeplog, Anonymous 1950–1983, 1984–1992). The outbreak periods of *M. pallipes* are shown by vertical lines.

no outbreaks developed in adjacent stands. From 1952 to 1993 there are no records of *M. pallipes* larvae south of the provinces of Värmland, Västmanland, and Uppland.

Larval feeding and effects on the tree

The feeding pattern in Uppland was similar to that which was observed in the outbreak areas. The young instars fed on needles and stems of the current year's shoots. Third stage and older larvae also utilised old foliage when the new foliage was depleted. At low attack densities, an aggregated distribution of larvae within crowns was clearly evident.

Tree mortality was sporadic, but the leading shoot died on many trees. Bark feeding on new shoots always occurred. At high attack densities, the many feeding patches resulted in girdling and drying out of entire shoots or of the apical portion. In the following year, such stems developed a rich growth from secondary buds.

M. pallipes larvae have been observed on *P. contorta* both in Lapland (Tärendö in 1986, Arvidsjaur in 1987) and in Uppland (Västland in 1989), but severe tree mortality did not occur. The observed damage at about equal larval densities was less severe on *P. contorta* than on *P. sylvestris* (Arvidsjaur in 1987).

Host relations and fecundity

At Forsmark, trees growing on wet sites, on dry sites on an old shore ridge, and on moderately moist sites, were attacked with about equal frequency during the outbreak years. Preference toward trees not forming stands and trees growing along edges and openings was evident during the declining phase of the outbreak.

Timing of emergence in relation to host development differed between years. In 1989, emergence began early and the newly emerged larvae fed on the stems of the young shoots as well as on the developing needles. In 1990, young needles were available on all trees at the time of hatching, and the newly emerged larvae fed mainly on these needles. In 1989, no differences were observed in the number of larvae on trees with early and late shoot development.

In Uppland, the average number of mature

Table 1. *Records of* M. pallipes *larvae in Sweden 1952 to 1992. Size of damaged area: 0 = a few trees in a stand or scattered trees not forming stands, 1 = < 1 ha, 2 = < 10 ha, 3 = < 100 ha, 4 = < 1000 ha. Damage categories: 0 = a few needles, 1 = many needles but few shoots entirely defoliated, 2 = many shoots defoliated but few leaders dying, 3 = many leaders but few trees dying, 4 = many trees dying, 5 = most trees dying. Source: KHF = Forsslund (1960); BE = Bengt Ehnström (pers. com.); BR = Birger Risberg (pers. com.); ÅL = Åke Lindelöv (pers. com.); JM = Forest Officer reports; EO = the author*

Province	Site	Year	Area	Damage	Source
Up	Älvkarleby	1981	0		BE
Up	Älvkarleby	1984	0		EO
Up	Forsmark	1989–92	3	3	EO
Up	Vattholma	1989–92	1	1	EO
Up	Västland	1989–92	1	1	EO
Up	Gimo	1991	0		EO
Up	Vätö	1992	0		ÅL
Vs	Skinnskatteberg	1987	0		EO
Vr	Filipstad	1988	0		EO
Vr	Filipstad	1992	1	1	EO
Dr	Lima	1960			KHF
Dr	Älvdalen	1952–56	4	4–5	KHF
Dr	Älvdalen	1974–76	3	2	EO
Dr	Älvdalen	1966–69	4	3–5	BE JM
Dr	Särna	1974–78	3	4	EO
Dr	Särna	1984	2	2	EO
Dr	Särna	1988	3	3	EO
Dr	Särna	1989–90	3	1	EO
Dr	Idre	1953–56	2	4	KHF
Dr	Idre	1967	4		JM
Dr	Idre	1974–76	3	3–4	EO
Hs	Ytterhogdal	1988	2	1	EO
Hs	Kårböle	1982	3	2–3	EO
Hs	Delsbo	1984	2	0	EO
Me	Långskog	1992	0		EO
Hr	Linsell	1953		2–3	KHF
Hr	Sveg	1988	2	3–4	EO
Jä	Kälarne	1990	1	4	EO
Ån	Bjurholm	1990	2	1	BR
Vb	Burträsk	1957–58		0–1	KHF
Vb	Jörn	1957		0–1	KHF
Vb	Fällfors	1958			KHF
Nb	Piteå	1958			KHF
Nb	Älvsbyn	1957		0–1	KHF
Nb	Vidsel	1975	0		EO
Nb	Boden	1990–91	0		EO
Nb	Selet	1957–58			KHF
Nb	Ljusåå	1958			KHF
Nb	Nederkalix	1957		0	KHF
Nb	Tärendö	1956			KHF
Nb	Tärendö	1986	1	2	EO
Nb	Muonio	1958–59			KHF
Ås	Almsele	1959	2	3	BE
Ly	Örträsk	1957–58		0–1	KHF
Ly	Lycksele	1957			KHF
Ly	Malå	1985–87	3	4–5	EO
Pi	Arvidsjaur	1955–59	4	4–5	KHF
Pi	Arvidsjaur	1965–67	4	3–5	JM
Pi	Arvidsjaur	1975–78	3	4	EO
Pi	Arvidsjaur	1985–88	4	3–5	EO
Pi	Grästjärn	1958			KHF
Pi	Arjeplog	1958–59	4	3–4	BE
Lu	Kåbdalis	1975	2	3	EO
Lu	Nattavaara	1955–57	4	4–5	KHF
Lu	Nattavaara	1975	3	4	EO
Lu	Gällivare	1955–58	4	4–5	KHF

Table 2. *Number of eggs in ovaries of* M. pallipes

Province and site		Year	Host	n	Developed eggs		Undeveloped eggs	
					Mean ± SD	Range	Mean ± SD	Range
Up	Västland	89	PC	39	92 ± 16	31–118	3 ± 2	0–10
Up	Västland	89	PS	27	93 ± 14	65–123	3 ± 3	0–10
Up	Forsmark	89	PS	100	76 ± 18	25–118	4 ± 2	0–11
Up	Forsmark	90	PS	120	93 ± 16	50–132	4 ± 3	0–14
Dr	Särna	90	PS	15	76 ± 15	49–111	3 ± 2	0–10
Pi	Arvidsjaur	85	PS	62	41 ± 13	12–65	2 ± 1	0–7

eggs in ovaries of newly emerged females varied between 76 and 93 (25–132; Table 2). A sample from Lapland contained 41 eggs (12–65). In a laboratory test, there was no difference in oviposition ability on *P. sylvestris* branches between four foliage types (ANOVA, $p=0.21$; Table 3). Oviposition began shortly after the adults were put on the foliage and was completed within 2 days. The number of deposited eggs was 74 ± 26 (24–119, $n=39$); 2–4 (0–14) eggs remained in the ovaries. There were no differences in egg development. Because no new growth was available, most larvae died shortly after hatching, but a few larvae on the soft, shaded foliage completed their development.

The effect of tree species on fecundity was studied at Västland, where larvae occurred on both *P. sylvestris* and on *P. contorta*. The sampled larvae were reared to cocoon-spinning on their respective host. The number of eggs in ovaries of newly emerged females did not differ between these groups (Table 2).

Young larvae were difficult to rear because of their dependence on fresh growth and their mobility, which tended to lead them away from the foliage. By contrast, older *M. pallipes* larvae accepted any fresh pine foliage. They were able to complete their development on drier foliage than larvae of *N. sertifer* (unpublished results). This resilience towards dry foliage was also observed in the outbreak areas.

Life history

A one-year life cycle dominated, but in all populations a varying proportion had a 2-year or longer development, depending on the length of the diapause in the cocoon. At Forsmark, the earliest adults were observed on 8 May 1990 and the latest on 9 June 1989. The swarming peak coincided with egg hatch of *N. sertifer* occurring in the same stands in both years. In the rearings, the emergence distributions were largely symmetrical, with durations of ca. 2 weeks and with no differences between males and females.

The longevity of the adults was not influenced by access to liquid food. They were not attracted by a sugar solution and no feeding was observed. Survival was 6.2 ± 1.4 days ($n=18$) without and

Table 3. *Number of eggs per* M. pallipes *female deposited on different types of pine foliage in a laboratory test*

Mature trees with large, coarse exposed needles	Mature tree with small, exposed needles	5 m trees with soft shaded needles	<0.5 m trees with exposed needles
70	42	95	24
57	28	57	85
70	89	100	mv[a]
84	119	81	24
101	73	110	67
40	89	66	50
93	70	86	105
100	118	111	70
24	74	66	50
58	87	77	78
Mean 69.7	78.9	84.9	61.4
SD 25.6	28.9	18.9	27.1
Range 24–101	28–119	57–111	24–105

[a] Missing value.

6.6 ± 1.2 days ($n = 18$) with access to the liquid dispensers.

Oviposition occurred in the previous year's needles before the current year's growth was available. In a sample of needles with eggs (Forsmark in 1990, $n = 375$), 66, 27, 5, and 2 per cent of the needles had 1, 2, 3, and 4 eggs, respectively. A needle that was not included in the samples had eight about equally spaced eggs. The egg pocket distributions (the distal egg when there were several on the same needle) in a field sample from Uppland (Forsmark in 1990) and in a laboratory-reared sample from Dalarna (Särna in 1975) were similar (Table 4). Both distributions peaked at 4 mm from the needle tip and were skewed toward the needle base. The distance between egg pockets on the same needle (Forsmark in 1990) was 1.8 ± 1.4 mm (0–5, $n = 162$). There were 16 ± 13 (1–49) eggs per shoot ($n = 34$), and 1.2 ± 0.6 needles with eggs per cm of shoot length ($n = 31$).

The time between the earliest field observation of newly emerged and mature fifth instar larvae was 37 days in 1989 and 47 days in 1990. Larvae were abundant during 60 and 70 days, respectively. In the middle of this period, all five larval instars were present on the trees. The development time of individual larvae was about the same as in *N. sertifer*. The oldest larval instar of *M. pallipes* occurring in abundance was two stages behind the *N. sertifer* larvae throughout development.

Extensive field searches to study the choice of cocoon-spinning sites yielded few cocoons. They were found in dry moss on the ground, below moss on stones, under bark of dry wood on the ground, and in bark crevices on trees in the litter layer. No cocoons were found on trees or elsewhere above ground.

After cocoon spinning, the field-sampled larvae invariably entered a diapause. Its induction was not influenced by the length of the photoperiod during the larval period (Table 5). In studies on other pine diprionids including *Diprion pini* (L.), *Diprion similis* (Htg), *Gilpinia frutetorum* (F.), *Gilpinia socia* (Kl.), *Gilpinia pallida* (Kl.), *Gilpinia virens* (Kl.), and *Gilpinia laricis* (Jur.), few larvae entered diapause when reared at a 22 h photoperiod (unpublished).

Table 5. *Comparison of cocoons obtained from larval samples from a* M. pallipes *(MP) population in Uppland reared at various photoperiods from the third larval stage*

	Photoperiod, hours			
	22	18	14	10
No. cocoons yr 1	224	234	227	232
Per cent MP emerged yr 2	79	79	78	87
Per cent MP in diapause yr 2	1	7	1	2
Per cent parasitoids	1	1	1	1
Per cent other mortality	20	12	20	10

At 4°C, the diapause was terminated in part of a sample after 2 months and in all individuals not in prolonged diapause after 4 months (Fig. 3). Prolonged diapause occurred in a low percentage in all samples and did not exceed 20 per cent (Tables 6, 7, and 8). Various daylength

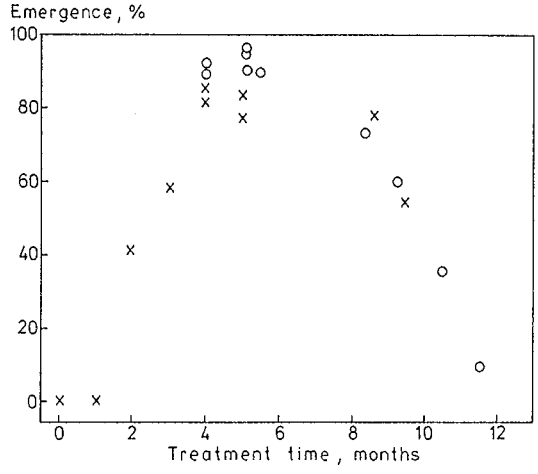

Fig. 3. Percentage emergence of *M. pallipes* from cocoons at 23°C and 22 h daylight after treatment for various periods at 4°C and 10 h daylight. Cocoons were obtained from larval samples collected at Forsmark. o = 1989, 100 cocoons/sample; x = 1990, 200 cocoons/sample.

Table 4. *Location of* M. pallipes *eggs on needles, measured as the distance (mm) from the needle tip to the leading edge of the egg pocket. The range and percentile values are shown*

Site	*n*	Min.	10%	50%	90%	Max.
Forsmark	375	2	3	5	7	23
Särna	270	2	4	5	16	35

Table 6. *Analyses of cocoons obtained from larval samples from three* M. pallipes *(MP) populations in the province of Uppland in 1989–1991*

	Stångskäret			Hällberget			Vattholma		
	1989	1990	1991	1989	1990	1991	1989	1990	1991
No. cocoons yr 1	889	471	211	220	252	137	150	140	142
Per cent MP emerged yr 2	92	83	69	91	81	74	69	50	25
Per cent MP in diapause yr 2	4	4	14	7	2	4	17	11	17
Per cent parasitoids[a]	2	8	15	1	14	17	8	16	53
Per cent other mortality	3	6	2	1	2	5	5	23	6
Parasitoid ratio[b]	0.01	0.08	0.13	0.01	0.16	0.21	0.07	0.27	1.50
MP diapause ratio[c]	0.04	0.04	0.17	0.07	0.03	0.06	0.20	0.19	0.17
MP female ratio[d]	0.58	0.57	0.42	0.59	0.53	0.50	0.67	0.57	0.56

[a] Prolonged diapause did not occur in the parasitoids.
[b] Ratio between parasitoid and *M. pallipes* emergence yr 2.
[c] Proportion in diapause of all living *M. pallipes* yr 2.
[d] Proportion females of all emerged *M. pallipes.*

Table 7. *Comparison of cocoons obtained from larval samples of* M. pallipes *(MP) from* P. sylvestris *and* P. contorta *at Västland in 1989*

	P. sylvestris	*P. contorta*
No. cocoons yr 1	93	89
Per cent MP emerged yr 2	46	63
Per cent MP in diapause yr 2	2	2
Per cent parasitoids[a]	39	19
Per cent other mortality	13	16
Parasitoid ratio[b]	0.14	0.05
MP diapause ratio[c]	0.02	0.02
MP female ratio[d]	0.70	0.70

[a] Prolonged diapause did not occur.
[b] Ratio between parasitoid and *M. pallipes* yr 2.
[c] Proportion in diapause of all living *M. pallipes* yr 2.
[d] Proportion females of all emerged *M. pallipes.*

Table 8. *Analyses of cocoons obtained from larval samples from a* M. pallipes *(MP) population in Uppland 1989 and 1990*

	1989				1990		
	9 July	15 July	22 July	27 July	4 July	16 July	6 Aug.
No. cocoons yr 1	202	399	155	133	171	172	128
Per cent MP emerged yr 2	97	95	85	86	84	83	80
Per cent MP in diapause yr 2	1	2	9	9	6	1	6
Per cent parasitoids	1	2	3	0	7	10	5
Per cent other mortality	2	2	3	5	4	6	10
Parasitoid ratio[a]	0.00	0.01	0.02	0.00	0.09	0.10	0.06
MP diapause ratio[b]	0.01	0.02	0.10	0.09	0.07	0.01	0.06
Parasitoid diapause ratio[c]	0.00	0.00	0.00	0.00	0.00	0.01	0.00
MP female ratio[d]	0.54	0.54	0.67	0.56	0.44	0.63	0.68

[a] Ratio between parasitoid and *M. pallipes* emergence yr 2.
[b] Proportion in diapausing of all living *M. pallipes* yr 2.
[c] Proportion in diapause of all living parasitoids yr 2.
[d] Proportion females of all emerged *M. pallipes.*

regimes during the last larval stages and the cocoon period had little effect on the incidence of prolonged diapause, although it was significantly larger at 18 h ($p<0.05$, Chi-square test; Table 5). In the samples from Dalarna and Lapland, prolonged diapause frequencies of less than 1 per cent and up to 75 per cent occurred (Table 9).

Following diapause termination after 4 months, morphogenesis was resumed. Post-

Table 9. *Analyses of cocoons obtained from larval samples from* M. pallipes *(MP) populations in Dalarna and Lapland*

	Arvidsjaur				Särna-Idre		
	1975	1976	1985	1987	1975	1976	1990
No. cocoon yr 1	300	1200	135	107	1200	700	194
Per cent MP emerged yr 2	64	36	65	7	5	20	17
Per cent MP in diapause yr 2	2	6	0	4	7	12	52
Per cent parasitoids	7	31	10	70	67	53	27
Per cent other mortality	27	27	24	20	21	15	4
Parasitoid ratio[a]	0.07	0.74	0.16	8.14	12.98	2.53	1.58
MP diapause ratio[b]	0.04	0.15	0.00	0.36	0.65	0.39	0.75
parasitoid diapause ratio[c]	0.00	0.01	0.00	0.00	0.02	0.01	0.00
MP female ratio[d]	0.73	0.62	0.84	0.14	0.43	0.59	0.45

[a] Ratio of parasitoids and *M. pallipes* emerged yr 2.
[b] Proportion in diapause of all living *M. pallipes* yr 2.
[c] Proportion in diapause of all living parasitoids yr 2.
[d] Proportion females of all emerged *M. pallipes*.

diapause development at 4°C was measured as time to emergence after transfer to 23°C. It was 21 days (13–28 days) after diapause termination, decreased linearly to 9 days after 4.5 months (Fig. 4, $r^2 = 0.987$), then levelled off to a minimum value of 7 days (Fig. 4). Mortality increased after 8 months at 4°C and reached 90 per cent after 11 months. Dissection of the intact cocoons showed that morphogenesis had been interrupted during the pupal stage. The ratio between the development rates at 23 and 4°C was 10.9. Assuming linearity, the developmental zero was 2.1°C. The number of degree-days to emergence was 440. Samples taken from 4°C and from the field on 12th April emerged after 11 (9–14, $n = 35$) and 12 days (9–16, $n = 30$), respectively (Fig. 4).

Emergence of insects in prolonged diapause was studied in the samples from the outbreak areas in 1975 and 1976 (Table 9). After a second hibernation there was a coherent emergence period in spring lasting 8 to 9 days. It coincided with the emergence period after a one-year hibernation in other samples.

Sex ratio could not be determined accurately by cocoon size, as with the larger pine sawflies. From small cocoons, assumed to be males, 7 per cent females emerged; male emergence from large cocoons was 4 per cent ($n = 27$). A further bias was caused by parasitism. In 24 of 25 samples more parasitoids emerged from small than from large cocoons. The ratio was 2.6 ± 1.6. The proportion of emerged females was 59 ± 6 per cent (44–70, $n = 27$).

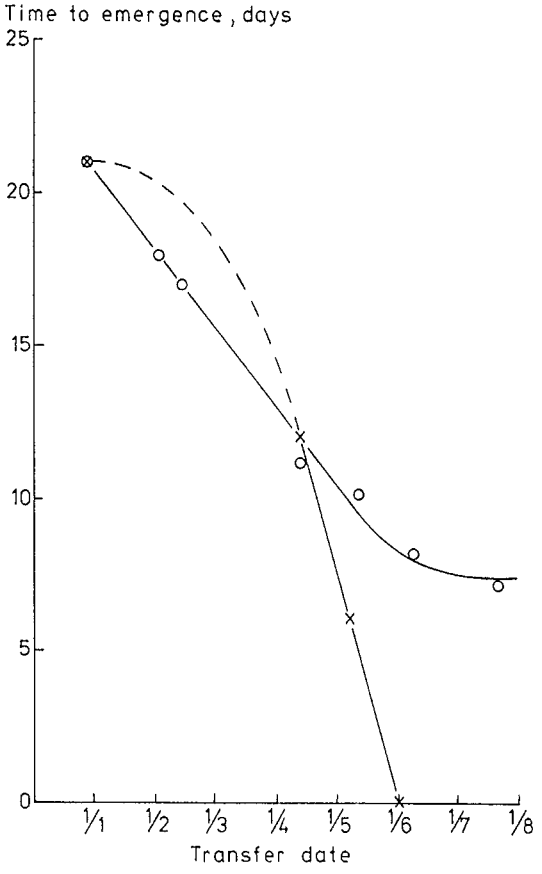

Fig. 4. Number of days to emergence of *M. pallipes* adults at 23°C and 22 h daylight after different periods at 4°C and 1 h daylight. Laboratory reared insects (o) are compared with a sample kept in the litter at Forsmark (x).

Mortality

Low temperature caused larval mortality at Arvidsjaur in 1987. Average monthly temperatures in July, August, and September were 11.8, 8.0, and 5.0°C respectively (at Storberg, Anon. 1987). The larvae developed slowly and remained in their fourth and fifth instars in September. Of larvae sampled on 11th September ($n=969$), 14 per cent were dead or dying and the others showed signs of starvation. They resumed feeding in the laboratory and there was only 5 per cent additional mortality (data on the cocoons in Table 9).

Twelve parasitoid species, six of which have not previously been reported as natural enemies of *M. pallipes* in Sweden, emerged in the rearings (Table 10). *Chrysonotomyia ruforum* (Krausse) is the only abundant parasitoid on diprionid eggs when *M. pallipes* eggs are available. Egg mortality in a field sample (Stångskäret 1990, $n=$ 536 eggs) was 11 per cent; 8.8 per cent were parasitised by *C. ruforum* and 2.1 per cent were dead from other causes.

Larval parasitism was low in the outbreak populations in Uppland (Tables 5–8), compared with Dalarna and Lapland (Table 9). It increased only slowly during the declining phase of the outbreak. Parasitism levels were higher in the low-density populations, and there was an increase between years at Vattholma (Table 6). The population at Västland also had a comparatively high level of parasitism. It was higher on *P. sylvestris* than on *P. contorta* ($p<0.01$, chi-square test; Table 7).

Rhorus substitutor (Thunb.) was the dominating larval parasitoid in all populations. Its development was mainly univoltine, but a low rate of prolonged diapause occurred (Tables 8, 9). Only 1.1 per cent of all emerged parasitoids ($n=$ 1950) belonged to other species (Tables 5–9). The number of specimens is shown within parentheses. Ichneumonidae: *Exenterus simplex* Thoms.: Up. Forsmark, Stångskäret 1989 (5); Hällberget 1989 (2); Up. Västland 1989, *P. contorta* (1), *P. sylvestris* (1). *Exenterus amictorius* (Panz.): Dr. Särna 1975 (1); Up. Vattholma 1990 (1); Up. Västland 1989, *P. sylvestris* (1). *Lamachus longiventris* (Thoms.): Pi. Arvidsjaur 1987 (2). *Olesicampe macellator* (Thunb.): Up. Forsmark, Stångskäret 1989 (1). Tachinidae: *Sturmia inconspicua* (Meig.): Dr. Särna 1975 (1); Up. Forsmark 1989 (1), 1990 (4); *Diplostichus janithrix* (Htg.): Up. Vattholma 1989 (1). The ectoparasitic larvae of *Adelognathus tetracinctorius* Thunb. (Ichneumonidae) were found in several localities but did not occur in the samples.

Few dead *M. pallipes* larvae were found on trees. The only pathogenic microorganism in samples of dead larvae ($n=340$) was midgut and hemocoelic invasion by flagellates of the Leptomonas type in one specimen (Lapland in 1981). There was no evidence of infectious disease in rearings of larvae collected during outbreaks in Lapland, Dalarna, and Uppland. In tests with three sawfly viruses, there were no external signs of disease and no evidence of infection in cells. *M. pallipes* larvae were susceptible to large deposits of *B. bassiana* spores on pine needles. In a laboratory test, 100 per cent mortality was obtained after 14 days in groups of 11 larvae ($n=14$).

Survival in planted cocoons was 13 per cent in 1989 (Table 11). In 1990, survival was 16 per cent during autumn and 12 per cent during winter-spring. By combining these data, a total survival of 2 per cent was obtained. Predation, mainly by small mammals, was the major cause of mortality.

Additional mortality was caused mainly by wireworms (Col., Elateridae). In 1989, mortality was 56 per cent during autumn, 50 per cent during winter-spring, and 78 per cent during the entire period. In 1990, autumn and winter-spring mortality was 68 per cent and 80 per cent, respectively. The combined mortality was 94 per cent. Parasitoids caused 11 per cent mortality during autumn. *Pleolophus basizonus* (Grav.) emerged from 9 cocoons in both 1989 and 1990. In 1990, *Dahlbominus fuscipennis* (Zett.) emerged from 6 cocoons. The 10 dead *M. pallipes* found in cocoons in 1991 (Table 11) were overgrown by a white mycelium. A sample grown on Saboraud-Maltose agar was identified as *B. bassiana*.

Discussion

Distribution and outbreaks

M. pallipes has been found in most Swedish provinces, but no previous observations of

Table 10. *Records of parasitoids on* M. pallipes. *PW = Pschorn–Walcher (1964), NM = Mallach (1974b), KHF = Forsslund (1960), EO = this study. E, L and C represent egg-, larval- and cocoon parasitoids respectively*

Parasitoid family and species	M.p. polita		M.p. pallipes	
	PW 1964	NM 1974	KHF 1960	EO
TETRACAMPIDAE				
Dipriocampe diprioni (Ferrière)		E		
EULOPHIDAE				
Chrysonotomyia ruforum (Krausse)	E	E		E
Neochryocharis formosa (Westwood)		E		
Dahlbominus fuscipennis (Zetterstedt)	C			C
Tetrastichus sp.		C		
PTEROMALIDAE				
Mesopolobus subfumatus (Ratzeburg)		C		
Habrocytus sp.		C		
Pteromalus sp.				C
TORYMIDAE				
Monodontomerus dentipes (Dalman)		C		
ICHNEUMONIDAE				
Ufam. Ephialtinae				
Itoplectis maculator (Fabricius)		C		
Itoplectis sp.		C		
Ufam. Tryphoninae				
Exenterus simplex Thomson	L		L	L
Exenterus abruptorius (Thunberg)	L			
Exenterus amictorius (Panzer)		L		L
Exenterus adspersus Hartig	L	L		
Ufam. Gelinae				
Pleolophus basizonus (Gravenhorst)	C		C	C
Pleolophus (*Aptesis*) spp.		C		
Agrothereutes abbreviator (Fabricius)		C		
Agrothereutes adustus (Gravenhorst)		C		
Gelis areator (Panzer)		C		
Gelis cursitans (Fabricius)		C		
Gelis instabilis (Förster)		C		
Gelis speculator (Förster)		C		
Gelis spp.		C	C	
Ufam Scolobatinae				
Hypsantyx lituratorius (Linnaeus)			L	
Zemiophora scutulata (Hartig)	L			
Lamachus longiventris Thomson			L	L
Lamachus eques (Hartig)	L			
Lamachus frutetorum (Hartig)		L		
Rhorus substitutor (Thunberg)	L		L	L
Ufam. Porizontinae				
Olesicampe macellator (Thunberg)			L	L
Ufam. Adelognathinae				
Adelognathus tetracinctorius (Thunberg)			L	L
TACHINIDAE				
Sturmia inconspicua (Meigen)	L	L		L
Blondelia inclusa (Hartig)	L	L	L	
Diplostichus janithrix (Hartig)				L

larvae were reported south of the outbreak area in Dalarna. Records from Skåne, Öland, Småland, Gotland, and Västergötland are based on museum specimens. The only previous record from Uppland was a male collected at Värmdö in 1937 (Forsslund, 1960). Whether there are low-density populations south of the provinces of Värmland, Västmanland and Uppland, is not known.

The distribution record of major outbreaks (Fig. 1) is considered to be complete from 1952 when Forsslund (1960) began his studies in the highland areas of Lapland and northwestern Dalarna. These areas, which are characterised by a continental type of climate (Ångström, 1958), have since suffered recurring outbreaks. The outbreak in Uppland is the only exception to this distribution pattern. There is no other

Table 11. *Mortality in* M. pallipes *cocoons attached by wire loops in litter below crown projection of young pine trees*

Cocoon contents	No. of cocoons			
	22/7 1989–14/9 1989 (54 d)[a]	22/7 1989–26/4 1990 (278 d)[b]	21/7 1990–17/9 1990 (58 d)[c]	26/9 1990–29/4 1991 (215 d)[d]
Samples size	135	135	135	133[e]
Intact cocoons				
M. pallipes	n.d.	18	22	16
M. pallipes, dead	n.d.	2	2	10
Parasitoids on larvae	n.d.	1	3	1
Parasitoids on cocoons	n.d.	9	15	0
Parasitoids, dead	n.d.	0	1	0
Opened, empty cocoons				
Insect predators	8	14	8	8
Mammal predators	67	91	84	98

[a] Predation marks checked and cocoons repositioned.
[b] Same cocoons as in previous column.
[c] Cocoons removed and contents examined.
[d] New cocoons put in same positions.
[e] Two cocoons were lost.

diprionid in Sweden with major outbreaks similarly restricted to geographically and climatically well defined areas.

There were several mass occurrences of diprionids in the outbreak areas in Dalarna and Lapland prior to 1952. The species were reported variously as *N. sertifer*, *D. pini*, or "pine sawflies" (Lekander, 1950). Because of their variability in colour, larvae of several of the diprionids occurring in northern Sweden would have been incorrectly identified if standard examination keys were used (cf. Forsslund, 1960). Thus the question whether there were *M. pallipes* outbreaks before 1952 cannot be resolved. However, it can be argued that there is a coincidence between an increasing number of large reforestation areas planted with pine in the outbreak areas (Stridsberg & Mattsson, 1980) and the onset of known *M. pallipes* outbreaks.

The four outbreak periods at Arvidsjaur coincide largely with the ten-year outbreak cycle of *Epirrita autumnata* (Bkh.) on mountain birch (Tenow, 1972 and personal communication). A correlation between outbreak periods of E. autumnata and low summer temperatures was related to weather effects on the host tree (Niemelä, 1980). A correlation with low summer temperatures is indicated in the outbreak data for *M. pallipes* (Fig. 2), but further outbreak cycles have to be studied to substantiate this. A hypothesis on interactions between weather and parasitism, that is consistent with such a correlation, is discussed below.

A correlation between weather and outbreaks is more likely to be manifest in *M. pallipes* than in *N. sertifer* populations in southern Sweden, because of the lower amplitude of the population fluctuations. This may be postulated on the basis of the large difference in carrying capacity between the stands usually attacked by *M. pallipes* and *N. sertifer*. In *M. pallipes*, severe defoliation of a young stand may occur at population densities between 10 000 and 100 000 larvae ha^{-1}. With a colonising density of 10–100 females ha^{-1}, a sequence of only two favourable years may result in a damaging outbreak. Most *N. sertifer* outbreaks occur in older stands, in which the amplitude of the population fluctuations is much larger. These populations have at least twice as long build-up periods to reach outbreak densities (unpublished data). The short build-up period, the less complex population system, and the more extreme weather variations in the outbreak areas, may contribute to a more direct link between weather and outbreak cycles in *M. pallipes* than in *N. sertifer*.

Relationships with the tree

Several factors contribute to make *M. pallipes* the most destructive among the Swedish pine sawflies: the feeding on the current year's foliage by young larvae, which is unique among the

diprionids in Sweden; the feeding on older needles by the later instars, which may result in complete defoliation; the wasteful feeding habit, whereby relatively few larvae completely defoliate a tree; the attacks on young plants, which are also unique among the Swedish diprionids; the attacks occur on poor sites with suppressed tree growth.

Bark feeding has not previously been emphasised as a major cause of mortality of young trees attacked by *M. pallipes*. Larvae of all pine diprionids feed on the bark of shoots. *N. sertifer* larvae feed mainly on the previous years' shoots, usually in relatively small amounts per larva, and mainly on the upper side of the branch. Therefore, girdling is infrequent. The other pine diprionids with gregarious larvae may feed on the bark of young shoots, but this occurs later in the season when the shoots are less sensitive. It becomes extensive only at high population densities. In contrast, *M. pallipes* larvae always feed heavily on the bark of the new shoots. On young trees, the leading shoot is usually attacked. The effect on the tree may be influenced by bark structure and stem circumference. This is consistent with the less severe damage on *P. contorta* compared to *P. sylvestris* and on the several metres tall trees affected in Uppland, compared to the smaller, less vigorously growing trees in the outbreak areas.

Food quality influences mortality of young *N. sertifer* larvae as well as their development time, although the effects were relatively small (Larsson, Björkman & Gref, 1986). In *M. pallipes*, no effects of previous defoliation on larval performance was reported (Niemelä, Tuomi, Mannila & Ojala, 1984). However, Lyytikäinen (1992) found that larval development in *M. pallipes* and *G. pallida* was slower when larvae were fed on foliage from damaged trees. Furthermore, larval growth was found to be slower and males were smaller when larvae were reared on foliage from young compared to old trees. This could indicate that the restriction of major outbreaks to reforestation areas is unrelated to properties of the trees.

Larvae of *M. polita* are considered to be gregarious, because the young first instars congregate at the empty egg pockets on old foliage (Mallach, 1974*a*). This was not observed in the rearings of *M. pallipes* on old foliage. Throughout their development, the larvae showed no tendency to remain near each other, neither did they show aversion during accidental encounters. However, many larvae may be found on the same shoot as a result of aggregated oviposition or high population levels.

Because of their dependence on young foliage, synchronisation with the host is more critical for survival of newly emerged larvae of *M. pallipes* than it is for the other pine diprionids. There was no indication of a differential survival related to tree phenology in Uppland. However, considering the earlier shoot development in southern pine provenances (Ståhl, 1984) and the data on diapause and morphogenesis in the cocoon, *M. pallipes* larvae would be expected to emerge quite early in relation to shoot development in the south of Sweden. There were no developmental differences between the samples from Uppland and the outbreak areas that indicate adaptations to different latitudes.

Abiotic conditions and life history

Because the diapause is broken during winter, the time of emergence is determined primarily by spring temperatures. In the outbreak areas, the adults occur mainly in June, while in Uppland, they fly mainly in May. The period during which adults were observed in the field was about twice as long as the emergence period in the laboratory. Thus, contrary to the bimodal pattern in *M. polita* (Pschorn–Walcher, 1987), *M. pallipes* has a continuous emergence period. The temperature required for development from pupa to adult is unknown. *M. polita* emerges at above 8°C (Mallach, 1974*a*).

As shown at Arvidsjaur in 1987, low temperatures may limit larval development in northern Sweden. Based on the condition of the larvae and the absence of warm weather after sampling, it was concluded that survival was low. Previous defoliation could have contributed to reduced larval growth (Lyytikäinen, 1992). Because the larvae were almost fully developed during this unusually cold summer, low temperature is unlikely to cause significant mortality in most years.

The diapause in the cocoon is concluded to be obligatory, since it was induced irrespective of day-length (Table 5). The other cocoon-overwintering diprionids in Europe, including *M. polita*, have a facultative diapause, which is

induced by short daylength (Mallach, 1974*a*; Pschorn–Walcher, 1982). In southern Sweden, *G. pallida* and possibly other species may have two generations in some years (Olofsson, 1991). Thus, *M. pallipes* is the only cocoon-overwintering diprionid in Europe that is not potentially multivoltine.

The diapause usually lasts 1 or 2 years but may be extended to 4 years (Forsslund, 1960). The highly variable frequency of prolonged diapause in northern Sweden indicates that the main survival value is unrelated to the occasional occurrence of cold summers. None of the tested photoperiods elicited the same high incidence of prolonged diapause that occurred in some field samples (Table 5). However, prolonged diapause was more frequent in years with much larval parasitism (Tables 6 and 9). For *D. pini*, in which a corresponding correlation has been reported, it was suggested that both variables are related to population density (Pschorn–Walcher, 1982). However, in Uppland, the low-density Vattholma population had a higher incidence of both parasitism and prolonged diapause, than the outbreak populations. Further, at Särna, both parasitism and prolonged diapause frequencies were high in years with low larval densities. A causal relationship between parasitism and prolonged diapause would have an adaptive value also at low host densities (see below). A possible stimulus could be the searching parasitoids, to which the larvae respond with defensive behaviour. Diapause length is concluded to be the most important life-cycle variable in relation to exposure to mortality risks.

Laboratory observations indicated that both males and females are agile fliers in comparison with the other pine sawflies. This is supported by their ability to invade large reforestation areas shortly after planting. In contrast, Mallach (1974*a*) reported *M. polita* females to be poor fliers. Based on the host tree niche and the flight ability of *M. pallipes*, it is concluded that spatial dynamics may be more prominent than with the other diprionids.

Fecundity and oviposition

The percentage of females was low in comparison with samples from *N. sertifer* populations (unpublished data). Because the sex-ratio may be influenced by differential mortality and by the proportion of unmated females producing male offspring, no conclusions can be drawn as to the nature of the difference.

Fecundity was more variable in *M. pallipes* than in *N. sertifer* (unpublished data). The extent of genetic variation is unknown. Variables influencing the quality and quantity of ingested needles, including provenance, site factors, and weather, could be important. In *N. sertifer*, food quality did not influence fecundity measured as cocoon weight (Larsson et al., 1986). In *M. pallipes*, the geographical, climatic, and host-tree restrictions suggest that the outbreak distribution may be influenced by such relationships. An alternative interpretation is discussed below.

In contrast to *M. pallipes*, *M. polita* deposits the eggs in colonies with several eggs on each needle (Forsslund, 1960; Mallach, 1974*a*). Because of this difference between the subspecies, the oviposition pattern on needles in Uppland was compared with data from the outbreak areas (Table 4). However, no difference was found. The tendency to aggregated oviposition on branches has not been reported previously in *M. pallipes*. Based on the average size of an egg deposit on the large trees at low attack densities, and the total number of eggs laid by a female, it was estimated that a female deposited 20 per cent of her eggs on one branch. The low variance in the number of eggs per centimetre of shoot length may indicate an underlying behavioural pattern during oviposition. This pattern may not have been apparent in the outbreak areas, if it occurs there, because mainly young trees at high population densities were studied.

In the oviposition experiment, there was no effect of shoot and needle structure. During oviposition, a superficial slit is made in the needle; little needle tissue is removed compared to *N. sertifer*, which positions the egg entirely within the needle. This may make *M. pallipes* less dependent on host structure, and presumably less energy is required for oviposition. In *M. polita*, an egg is laid every second minute (Mallach, 1974*a*). It is concluded that host factors are unlikely to provide major constraints on oviposition ability.

Mortality of eggs

M. pallipes eggs, which protrude from the egg pockets, are readily available for generalist pred-

ators. However, their short development time and their spatial distribution reduce the likelihood of predation. Egg mortality, that may have been caused by predation, was low in the present study, and there are no other indications that such mortality is important.

Eggs parasitised by *C. ruforum* are conspicuous by their black chorion, contrasting with the whitish-yellow colour of healthy eggs. They are unlikely to be overlooked. However, no egg parasitism has previously been reported in *M. pallipes* in Sweden, while it is known to occur in *M. polita* (Table 10). An explanation may be that *N. sertifer*, the winter host of the bivoltine *C. ruforum*, is rare in the outbreak areas. It is concluded that egg parasitoids have a negligible influence on populations in the outbreak areas. However, in southern Sweden, where *N. sertifer* is common, *C. ruforum* could be an important component in the natural enemy guild of *M. pallipes*, as indicated by the results at Forsmark.

Mortality of larvae

In contrast to other pine diprionids in Sweden, *M. pallipes* has one dominant parasitoid species. In the studies by Forsslund (1960) *R. substitutor* caused 94 per cent of the total larval parasitism compared to 99 per cent in the present study. The results from Uppland showed that *R. substitutor* is distributed outside the outbreak areas. Both the comparatively high and increasing level of parasitism in the low-density Vattholma population (Table 6), where there was no evidence of outbreaks, and the high level of parasitism in Dalarna during a period with low population densities (Särna-Idre 1990, Table 9), indicate that *R. substitutor* is efficient at locating its host at low densities. The rapid increase during *M. pallipes* outbreaks (Arvidsjaur, Table 9) indicates its ability to track population changes of its main host.

The only other diprionid from which *R. substitutor* has been reared in abundance is *G. pallida* (Kl.) (Forsslund, 1960; Olofsson unpublished). It is noteworthy that *G. pallida* is the most frequent of the other diprionids in the outbreak areas, particularly when the trees have grown past the size at which they are severely attacked by *M. pallipes*. *R. substitutor* has also been reported from *D. pini* (Pschorn–Walcher, 1987). Its presence in all studied *M. pallipes* populations, the few records from other hosts, and the failure to parasitise *N. sertifer* larvae, show that *R. substitutor* is highly specialised on *M. pallipes*.

The higher percentage of larval parasitoids that emerged from small, as compared to large, cocoons indicates that parasitism caused a reduction in host size. Because oviposition by *R. substitutor* occurred during the earliest larval instars, it is unlikely that the behaviour of the parasitoid is related to the final size attained by the larvae. A higher frequency of parasitoid emergence from small cocoons has also been found in *D. pini* (Pschorn–Walcher, 1982).

In *M. polita*, suspensions of the *N. sertifer* NPV caused dose-related mortality of larvae at high doses with no evidence of cellular infections (Lobinger & Skatulla, 1989), while the tests with diprionid NPVs on *M. pallipes* were negative. Trypanosomatid flagellates, which were found in one larva, may be mildly pathogenic in sawflies (Smirnoff, 1974). *Beauveria* infections are infrequent in diprionid larvae in Sweden (unpublished data). Thus, there is no evidence that infectious diseases significantly influence survival of *M. pallipes* larvae.

Mortality of eonymphs, pupae, and adults

Little is known about mortality during the non-feeding cocoon-spinning instars. Some are likely to be eaten by birds, small mammals, and invertebrate predators. Although exceptional years with high mortality may occur, such predation is unlikely to be a major variable, owing to the short duration of this stage. Low temperatures during autumn may result in mortality resulting from impaired cocoon-spinning; however, the temperature requirement for spinning cocoons is not known.

The level of mortality in the cocoons in the upper ground layers was similar to that which has been found in other studies of pine sawflies (Pschorn–Walcher, 1982; Hanski, 1987; Olofsson, 1987) including *M. polita* (Mallach, 1974*b*). Small mammals caused the largest mortality, both during autumn and during winter-spring. The high mortality is unlikely to have resulted from a strong functional response to the relatively low densities of *M. pallipes* cocoons. Although it is not known how accurately

these data estimate the actual mortalities of the field population, the mortality during the cocoon stage is considered to be an important population variable. In the outbreak areas in Dalarna and Lapland, predation levels may be lower because of the less diverse habitats, which support fewer generalist predators.

Cocoon parasitism occurred only during autumn in this study (Table 10), but could presumably occur in spring as well. The cocoon parasitoid guild was essentially the same as for other pine sawflies (Oehlke, 1965). The level of parasitism during the cocoon stage may have been between 11 and 41 per cent, depending on which assumptions are made regarding interactions between the mortality factors (Table 11). Parasitism could have been higher than the recorded value, if factors influencing the probability of the finding of cocoons by parasitoids and predators coincided.

Mortality caused by fungal pathogens, which was low in this study, may be expected to vary between sites and years. Mallach (1974*b*) found between 6 and 12 per cent of cocoons with larvae overgrown by fungi in *M. polita*. The highest percentage was found in a moist site. Fungal pathogens are unlikely mortality agents in the often dry outbreak areas, but could be more important elsewhere.

No data are available on mortality of the adults. Predation by insectivorous birds and insects may occur, but significant effects on the *M. pallipes* populations are considered to be unlikely.

Interactions

Factors affecting larval growth may influence mortality when summer temperatures are too low to allow larval development to be completed. Effects of the highly variable summer temperatures within and between years in the outbreak areas may also be mediated by interactions with other organisms. As the larvae have no major enemies other than *R. substitutor*, which attacks the young larvae, the mortality during a prolonged period on the trees is unlikely to be larger than while the corresponding time is spent in the cocoon. However, parasitism by *R. substitutor* may provide a link between weather and *M. pallipes* population levels, related to dispersal. When an early warm period, allowing *M. pallipes* to colonise young stands, is followed by cold weather, which restricts the dispersal of *R. substitutor*, a rapid population increase in the colonised stands would be likely.

The very low level of prolonged diapause in *R. substitutor* contrasts with the frequently high level in *M. pallipes*. Because of the correlation between high frequencies of prolonged diapause in *M. pallipes* and parasitism, prolonged diapause provides an escape from the high parasitism pressure in the following year. This may contribute to increased stability, by preventing *M. pallipes* populations from being suppressed to very low levels.

Competition between natural enemies is unlikely during the egg and larval stages. During the cocoon period, there may be interactions, both between the different species of cocoon parasitoids, and between cocoon and larval parasitoids, in consequnce of hyperparasitism (Pschorn–Walcher, 1988). Further, predators which attack the sawfly cocoons may cause considerable mortality of the parasitoids.

Interactions related to the population levels of other diprionids through shared natural enemies may be important (Pschorn–Walcher, 1962), particularly outside the outbreak areas. In low-laying areas in northern Sweden, both *G. pallida* and *D. pini* occur. Farther south, several other diprionids become increasingly abundant, in particular *N. sertifer*. Interactions involving the egg parasitoid *C. ruforum* have been discussed above. The parasitoids on larvae of diprionids other than *M. pallipes* are unlikely to search on young trees on which few hosts would be found, but they may have some importance when *M. pallipes* larvae occur on larger trees. In the outbreak areas, the ability of *R. substitutor* to parasitise *G. pallida* may be important in maintaining its populations when *M. pallipes* larvae are scarce.

During outbreaks, the population density per unit area is much lower in *M. pallipes* than in the other pine sawflies. Studies of *N. sertifer* (Hanski, 1987; Olofsson, 1987) indicate that strong density-dependence in relation to small mammals is unlikely at such population levels. However, there may be interactions with population densities of other diprionids, to the extent that cocoons of different species contribute to a common functional response of the small mammal predators and the generalist cocoon

parasitoids. Thus, where other sawfly species occur, low populations of *M. pallipes* may suffer a higher mortality during the cocoon period than their own density would elicit.

Conclusions

In relation to the population dynamics of *M. pallipes*, three zones may be recognised in Sweden. (1) The provinces south of Värmland, Västmanland, and Uppland, (2) The areas from these provinces northwards outside the outbreak areas, (3) the outbreak areas in northwestern Dalarna and the inland areas of Lapland.

In areas characterised by low population densities, the population processes of *M. pallipes* may be similar to those of the other solitary diprionids, which never have attained outbreak densities in Sweden. Factors contributing to keep the populations low may be the larger variety and higher population levels of natural enemies, some of which are related to the population density of other diprionids. In particular, the overwintering mortality is likely to be important. Furthermore, parasitism by *R. substitutor* was frequently high also outside the outbreak areas. The scattered occurrence of high populations of *M. pallipes* on young plants on marginal sites is consistent with the hypothesis of interactions with other diprionids. In the south of Sweden, synchronisation with host development may restrict the abundance of *M. pallipes*.

The most prominent characteristic of the outbreak areas may be their unsuitability for other sawfly species, hence their support of few generalist diprionid parasitoids. In addition, the soil ecosystem is comparatively simple in these areas, with low levels of predators in most years. Thus, the populations in the outbreak areas would be influenced by comparatively few factors. The density-dependent mortality caused by *R. substitutor* was identified as a major component in this system. Spatial dynamics, interactions with weather, and the different diapause strategies of the host and the parasitoid, may be the major factors behind the outbreak cycles of *M. pallipes*.

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